

Mormoops blainvillii.

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Mormoops blainvillii Leach, 1821

Antillean Ghost-faced Bat

Aello Cuvieri Leach, 1821a:71. Type locality not specified. Restricted to Jamaica by Smith (1972:108).

Mormoops Blainvillii Leach, 1821b:77. Type locality, Jamaica.

Lobostoma cinnamomea Gundlach, 1840:357. Type locality, Catedral St. Antonio el Fundador, Canimar, Matanzas, Cuba.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Mormoopidae, Subfamily Chilonycterinae, Genus *Mormoops*. Two subspecies have been described, but Smith (1972) considers the species to be monotypic.

DIAGNOSIS. *Mormoops blainvillii* is smaller than its congener, *M. megalophylla*. Length of forearm ranges from 44 to 49 mm in *M. blainvillii*, shorter than the 50 to 61 mm range in *M. megalophylla*. Condylbasal length ranges from 12.7 to 13.7 mm, compared to 13.6 to 15.1 mm in *M. megalophylla*. In both species, the rounded pinnae are connected dorsally; in *M. blainvillii*, the connection is an inconspicuous band between the ears, whereas a prominent band between the pinnae fuses on the rostrum in *M. megalophylla*. The tragus of *M. blainvillii* has a lanceolate primary lobe, a small secondary fold medially, and a ventral projection. In *M. megalophylla*, the primary lobe is blunt, the secondary fold more complex, and the ventral projection smaller. The calvaria of *M. blainvillii* has a flattened frontal region and narrow rostrum as compared to a more rounded frontal and broad rostrum in the congener. In *M. blainvillii* the basioccipital and basisphenoid are narrow, and a narrow trough separates the auditory bullae. These features differ in *M. megalophylla*, in which the basioccipital and basisphenoid are broad with a longitudinal, median septum in the trough between the bullae (Smith, 1972).

GENERAL CHARACTERS. Individuals range from pale cinnamon to reddish cinnamon in color and are slightly darker dorsally than ventrally; no geographic variation in color has been described (Silva Taboada, 1979). Means of measurements (in mm, with ranges in parentheses) for 11 adult males (sample sizes in brackets if different) from Puerto Rico were: length of forearm, 46.7 (44.8–48.2); zygomatic breadth, 8.5 (8.4–8.8 [10]); rostral breadth, 6.8 (6.6–7.0); length of maxillary tooth row, 7.6 (7.5–7.8); and condylbasal length, 13.3 (13.0–13.5 [10]); for six males from Hispaniola: length of forearm, 47.2 (46.2–49.0); zygomatic breadth, 8.6 (8.4–8.9); rostral breadth, 6.7 (6.5–6.9); length of maxillary tooth row, 7.6 (7.4–7.8) [7]; and condylbasal length, 13.3 (12.8–13.7); for eight males from Jamaica: length of forearm, 46.6 (45.7–47.2); zygomatic breadth, 8.5 (8.3–8.8); rostral breadth, 6.5 (6.1–6.7); length of maxillary tooth row, 7.4 (7.2–7.7); and condylbasal length, 13.0 (12.8–13.4); and for six males from Cuba: length of forearm, 45.8 (44.8–46.6 [9]); zygomatic breadth, 8.3, (8.0–8.6); rostral breadth, 6.5 (6.3–6.6); length of maxillary tooth row, 7.3 (7.2–7.5); and condylbasal length, 12.8 (12.6–13.0; Smith, 1972). Additional mean measurements (with ranges in parentheses and sample sizes in brackets) of bats from Cuba were: length of humerus, 26.7 mm (25.3–28.6) [43 males, 43 females]; mass (from November to April), 8.0 g (6.8–9.3) [75 males, 39 females]; and wing area, 149.9 mm² (142.8–162.4) [15 males, 15 females] (Silva Taboada, 1979). Masses of 52 bats (both males and females) from Puerto Rico averaged 8.6 g (*SE* = 0.94; Rodríguez-Durán, 1995). External measurements (in mm, with ranges in parentheses) of five females from Puerto Rico were: total length, 83.8 (80–86); length of tail vertebrae, 29 (28–30); length of hind foot, 10.5 (10–11); and length of forearm 46.7 (46–48; Anthony, 1918). Smith (1972) reported clinal variation in size among the four island populations with the smallest specimens from Cuba and the largest from Puerto

Rico. However, standard measurements of a larger sample from Cuba reported by Silva Taboada (1979) spanned almost the entire size range of the species given by Smith (1972). Hall and Kelson (1959) placed Cuban and Jamaican populations into separate subspecies based on the shape of the first upper premolar; this distinction was rejected by Smith (1972) and Hall (1981).

DISTRIBUTION. The Antillean ghost-faced bat is known from the Greater Antilles, including Cuba, Jamaica, Hispaniola and Puerto Rico, and Mona Island west of Puerto Rico (Fig. 3; Koopman, 1951; Morgan and Woods, 1986; Olson and Pregill, 1982; Silva Taboada, 1974, 1979; Smith, 1972; Steadman et al., 1984).

FOSSIL RECORD. Fossilized remains of this species are limited but indicate a range that once extended to other Caribbean islands and the Bahamas. A fragment of a mandible was reported from pre-Columbian deposits of Exuma Island (Koopman, 1951; Koopman et al., 1957), and specimens are known from New Providence Island in the Bahamas (Olson and Pregill, 1982). Records from Antigua (Steadman et al., 1984) and Barbuda (Morgan and Woods, 1986) extend the historical range eastward into the northern Lesser Antilles (Fig. 3). Within the Greater Antilles, records include a fragmentary skull recovered from a cave deposit on Gonave Island, west of Hispaniola (Koopman, 1955), partial mandibles from Jamaica (Koopman and Williams, 1951), and skulls from a cave in north-central Haiti (Miller, 1929). Three authors have reported subfossil remains of *M. blainvillii* from Puerto Rico. Gundlach (1878: 140) reported specimens from “la parte meridional de la Isla,” Anthony (1918) recovered specimens from Cueva de Trujillo Alto, and Choate and Birney (1968) examined two complete and two partial crania from pre-Columbian deposits of Cueva de Clara. Cranial and postcranial remains were described from cave deposits in central Cuba that Silva Taboada (1974) postulated as late Pleistocene in age. Although the remains were significantly smaller than Recent *M. blainvillii*, Silva Taboada (1974) considered them conspecific.



FIG. 1. Antillean ghost-faced bat, *Mormoops blainvillii* from Manchester Parish, Jamaica. Photograph provided by H.-U. Schnitzler.

FORM AND FUNCTION. The thick, soft pelage of *M. blainvillii* is longer dorsally than ventrally; hair lengths range from 6 to 11 mm. Dorsal hairs are bicolored and darker toward the apex, whereas ventral hairs are more uniform. Downy fur covers the ventral surface of the wing proximal to the body. Three intergrading phases occur in the pelage of adults collected in April, May, July, and October to December ($n = 133$): snuff brown/cinnamon buff, Prout's brown/tawny olive, and argus brown/amber brown. Of these, the cinnamon buff phase was found exclusively in males and only in some months (April, May, October and November). In all months and in both sexes, the proportion of specimens in Prout's brown phase approximated that of the argus brown phase. No molting specimens were observed (Silva Taboada, 1979).

Elaborate facial excrescences and leaflike appendages distinguish both species of *Mormoops* (Fig. 1). The complex labio-nasal plate has fleshy papillae lateral to nostrils and irregular tubercles on the margin; nostrils are on fleshy pads separated by a median ridge. Intricate folds and scallops of the lower lip form shield-like plates covered with tubercles. A transverse fold separates this plate into an upper portion and a paired lower portion. Coarse bristles emanate from both lips. The lower edge of the pinna is broad and shelf-like, and confluent with the lower lip; the eye is located in the enclosure made by the pinna (Anthony, 1918; Smith, 1972).

The dental formula is $i\ 2/2$, $c\ 1/1$, $p\ 2/3$, $m\ 3/3$, total 34. Expanded crowns of bilobed upper medial incisors occlude with lower members and are much larger than the minute lateral incisors. A diastema separates lateral incisors and canines. The long, compressed canine has sharp edges both craniad and caudad. The first upper premolar is low-crowned with a sharp median cusp; the second premolar has the highest crown of the molar series. The first and second molars are approximately equal in size and dilambdodont, similar to *Pteronotus*. The third molar is approximately half the size of the second. Lower incisors, approximately equal in size, fill the space between the canines. Their edges are sharp and trilobed. The lower canine is simple. Each of the three lower premolars has a single trenchant cusp; the second is smaller than the others. The three lower molars are similar in form and of similar size (Anthony, 1918).

Members of the genus *Mormoops* have an unusual skull in which the rostrum is strongly upturned. The frontals rise abruptly from the rostrum and the two surfaces form an angle of nearly 90° (Fig. 2). The rostrum is about as broad as long with a median nasal depression. The zygomatic arch is not expanded laterally and the mastoid process is reduced. The incisive foramina are large and the palate is long and narrow. The mandible has a bend between the coronoid process and the third molar corresponding to the angle between the calvaria and rostrum. The coronoid process is low, but the mandibular condyle rises above the molar plane (Anthony, 1918; Smith, 1972).

Vaughan and Bateman (1970) described forelimb morphology of the Mormoopidae and, although most of their descriptions were based on *M. megalophylla*, the main features also apply to *M. blainvillii*. Adaptations to reduce weight characterize the wings of *Mormoops*. Some muscles of the wing are reduced or absent as compared to the Phyllostomidae. This simplification results in multiple functions ascribed to fewer muscles. Forearm muscles originate away from the center of rotation of the elbow, such that they are stretched upon flexion of the elbow. The long olecranon process, in combination with unusual curvature of the proximal end of the radius, increases the mechanical advantage of the triceps without sacrificing range of extension. These features contribute to automatic flexion and extension of distal wing elements following the actions of proximal muscles. Vaughan and Bateman (1970) consider that these characteristics enhance flight endurance and are adaptive for the aerial insectivorous niche of the Mormoopidae. The aspect ratio of the wings of one Antillean ghost-faced bat was 6.32, similar to *M. megalophylla*, but "its wing loading is a third lower (4.99 Nt/m^2)" (Smith and Starret, 1979:267).

The basal metabolic rate of 13 *Mormoops blainvillii* from Puerto Rico averaged $0.93\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$ ($SD = 0.29$), 48% of the predicted value for a eutherian mammal of its mass. The thermoneutral zone extended from 31°C to 34°C . Over a wide range of ambient temperatures (15°C to 41°C), most individuals maintained body temperature between 31°C and 34°C ; at ambient temperatures below 28°C , body temperature was less stable, decreasing in some to 25°C . *M. blainvillii* elevated its basal metabolic rate in response to these low ambient temperatures (Rodríguez-Durán, 1995). The



FIG. 2. Dorsal, ventral and lateral views of skull and lateral view of mandible of *Mormoops blainvillii* from Trelawny Parish, Jamaica (male, National Museum of Natural History 511226). Greatest length of skull is 14.1 mm. Photographs provided by Charles Handley.

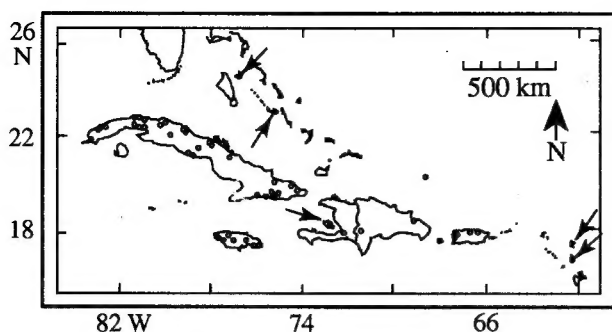


FIG. 3. Distribution of *Mormoops blainvillii*. Open circles represent Recent records; arrows indicate fossil records (references in text).

body temperature ($n = 301$) of bats leaving a cave in Cuba (38.8°C) differed from those entering the cave (37.9°C) and varied from winter (November to April, 37.4°C) to spring (May to October, 38.8°C ; Silva Taboada, 1979).

ONTOGENY AND REPRODUCTION. In Cuba, copulation begins in January and February. Pregnancies occur from March to June, with a maximum (90%) in May. The earliest birth was on 13 June, with records of young bats and lactating females from then until September. Weaning peaked from August to September, and from October until December females were in non-reproductive condition (Silva Taboada, 1979). The Antillean ghost-faced bat is monestrous and typically bears one young per year. Twins were reported in two instances (Gundlach, 1877; Silva Taboada, 1979). In one case, the combined mass of the twins was 2.5 g, corresponding to 31% of the female's body mass. Each one measured 17.5 mm in length (Silva Taboada, 1979). Body length and mass of embryos ($n = 38$) increased gradually from March (<4 mm and <0.4 g, $n = 3$) to June (20–27 mm and 1.6–2.7 g, $n = 8$). Most embryos examined were hairless with the exception of bristles around their snout and their feet. Juvenile bats collected in August ($n = 36$) were similar in color and mass to adult bats, but epiphyses were not completely ossified. The dentition of these juveniles was functional, but still developing (eruptive phase). The dentition of one bat collected in August was in the prefunctional eruptive phase. Testis size does not vary substantially during the year (Silva Taboada, 1979).

On one occasion (14 June), one female *M. blainvillii* in Cuba was observed carrying a newborn young into the day roost. It was unclear whether the female had carried her young with her all night on the foraging flight (Silva Taboada, 1979).

ECOLOGY. Analysis of stomach contents ($n = 49$) revealed that *M. blainvillii* feeds exclusively on insects. In Cuba, stomach contents collected in January, February, June and August to November contained Lepidoptera, suggesting that this bat feeds predominantly on this group. This may account for the characteristic coloration and consistency of stomach contents as compared to any other insectivorous bat in Cuba, except *Macrotus*. Samples also contained Homoptera (10.5%) and Coleoptera (5.3%). Stomach contents from Antillean ghost-faced bats collected at a day roost averaged 6% of body mass with a maximum of 14.7% (Silva Taboada, 1979). These bats catch insects in the air with a large pouch formed by the huge tail membrane (Schnitzler et al., 1991; Silva Taboada, 1979). *M. blainvillii* sometimes uses a wing to funnel an insect into the pouch.

Large populations of *Mormoops blainvillii* occur in appropriate habitats (Goodwin, 1970; Silva Taboada, 1979). In Cuba, some groups consist of 10,000 to 15,000 individuals, although others may number only in the hundreds. Small groups and single individuals are occasionally found in windy cave environments (Silva Taboada, 1979). The population using Cucaracha Cave (Puerto Rico) as a day roost in April, 1983 was estimated at 43,400, comprising approximately 6% of bats counted (Rodríguez-Durán and Lewis, 1987). In Jamaica, Goodwin (1970) estimated the population in Oxford Cave at 3,000.

The Antillean ghost-faced bat roosts exclusively in caves or abandoned mine shafts, typically in places with a stable microcli-

mate such as hot caves ("cuevas calientes"). In Jamaica, Goodwin (1970) reported that *M. blainvillii* penetrates farther into caves than other species, freely entering the smallest chambers and crawl ways. They also roost in less sheltered caves, or near the entrance of caves or mine shafts. In Cuba, *M. blainvillii* occurs most often in caves with a single entrance (80.6%), as compared to caves with multiple entrances (19.4%; Silva Taboada, 1979; McFarlane, 1986; Rodríguez-Durán, 1991, 1995).

Mormoops blainvillii coexists with other bats, but it does not appear to mix with other species. Groups roost primarily on cave ceilings and maintain distance between each other. Colonies frequently change roost sites within the same cave and may migrate between caves. In dark and sheltered caves, Antillean ghost-faced bats stay relatively alert during the daytime, but when disturbed they do not take flight as readily as other small mormoopids (*Pteronotus* sp.). When roosting in more exposed environments, they may become lethargic and recover only slowly when disturbed (Gundlach, 1877; Rodríguez-Durán, 1991; Silva Taboada, 1979). Sexual segregation may occur in conjunction with reproduction, but aside from this, mixed sex assemblages appear to predominate. In Jamaica, the sex ratio in four caves in January was nearly one to one (Goodwin, 1970).

Numerous parasites associate with *M. blainvillii* (summarized in Silva Taboada, 1979). Internal parasites include trematodes (*Ochoterenatrema diminutum*, *O. pricei*, *Parabascus cubensis*, *Anenterotrema auritus*), cestodes (*Vampirolepis* sp.), and nematodes (*Physicocephalus sexalatus*, *Capillaria pusilla*). External parasites incorporate several arachnids (*Cameronieta standtmanni*, *Antricola silvai*, *Parantricola marginatus*, *Lawrenceocarpus mormoops* (Cerny, 1967, 1969; de la Cruz, 1974; Dusbabek, 1967; Groschaft and Del Valle, 1969).

BEHAVIOR. A strictly nocturnal species, *M. blainvillii* remains in the day roost until after sunset (Miller, 1904). Time of first emergence varies and egress lasts from two to three hours; the bats exit sporadically. In Cuba, from February to December, mist net samples ($n = 12$) near roosts indicate that the onset of activity varies from 22–55 minutes after sunset. In Cucaracha Cave, Puerto Rico, *M. blainvillii* is the last (of four) species to exit, approximately 90 minutes after sunset (Rodríguez-Durán and Lewis, 1987; Silva Taboada, 1979). Late emergence may relate to the peak activity of Lepidoptera (Silva Taboada, 1979). Bats enter and leave the cave throughout the night, presumably on multiple feeding bouts, and appear to spend at least five hours out of the roost. Final return to the roost ($n = 9$) comes 10 to 44 min before sunrise, always at a light level of 0 lux (Silva Taboada, 1979).

The flight of *M. blainvillii* is faster and higher than that of other sympatric mormoopids (Goodwin, 1970; Silva Taboada, 1979). Flight speed is highest when the bats leave the cave and less when they return (Silva Taboada, 1979). A distinct humming sound is associated with its flight (Goodwin, 1970; Silva Taboada, 1979). Wing morphology and preliminary observations in Jamaica suggest that Antillean ghost-faced bats may forage close to the vegetation at forest edges and around tree crowns (Schnitzler et al., 1991; Silva Taboada, 1979).

As in other echolocating bats, biosonar vocalizations in *M. blainvillii* can be separated into three phases, as the bat searches for a target, approaches a target, and makes a terminal approach. In a flight cage, Antillean ghost-faced bats selectively hunted for moths, producing search-phase signals that changed from a shallow to a steep FM-sweep. Sometimes a brief, steep FM sweep preceded the shallow sweep. Search-phase signals had an average duration of 1.8 ms and an average interval of 55.4 ms. Signals contained 3–4 harmonics with energy concentrated in the second or third harmonic; the second harmonic ranged from 68–49 kHz. Upon approaching an insect, bats reduced signal duration and pulse interval. In the terminal phase they produced up to 38 calls with an average duration of 1 ms at an average pulse interval of 7.7 ms (Schnitzler et al., 1991).

GENETICS. The karyotype of *M. blainvillii* has a diploid number of 38 and fundamental number of 60. There are four pairs of metacentric, eight pairs of submetacentric and six pairs of acrocentric chromosomes. The species has a submetacentric X chromosome and an acrocentric Y (Nagorsen and Peterson, 1975). Its G-banded karyotype differs from confamilials by having four G-positive bands on arm 9, three of which are prominent. Both species



FIG. 4. G-banded karyotype of *Mormoops blainvillii* from St. Catherine Parish, Jamaica (male, Carnegie Museum of Natural History 44131). From Sites et al. (1981), with permission.

of *Mormoops* differ from *Pteronotus* sp. by having a prominent G-positive band near the centromere of arm 2 of chromosome pair 6 (arrow in Fig. 4). This may represent an euchromatic addition and is considered a derived condition for the genus (Sites et al., 1981). Three pairs of rDNA sites were identified on the short arms of small to medium sized chromosomes of *M. blainvillii*. This number is greater than the average for bats (1.76) but less than that in a sample of rodents (4.19; Baker et al., 1992).

REMARKS. The generic epithet, *Mormoops*, derives from the Greek roots *mormo*, a hideous monster, a hobgoblin, and *opsis*, aspect, appearance (Gotch, 1979). Leach (1821b) named the species in honor of Henri M. D. de Blainville (1777–1850), French physician and naturalist. The complex nomenclatural history of the genus *Mormoops* was recounted by Rezsutek and Cameron (1993). Hall (1981) referred to the Antillean Ghost-faced bat as *Aello cuvieri* in spite of the long-standing use of *Mormoops blainvillii*, and its official recognition by the International Commission of Zoological Nomenclature (Opinion 462, International Commission of Zoological Nomenclature, 1957). Novick (1971) notes that *Mormoops* does not survive in captivity.

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